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OF THE

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Vol. 49 No. 5

BULLETIN

OF THE

TORREY BOTANICAL CLUB

MAY, 1922

New British and American species of Lobomonas: a study in morphogenesis of motile algae

TRACY E. HAZEN

(WITH PLATES 5 AND 6)

The genus *Lobomonas* was established in 1899 by Dangeard (**3**) on a single species, *L. Francei*, found somewhat frequently in the vicinity of Poitiers, France. This species had been figured twenty-one years previously by Stein (**7**, *pl. 13, f. 17, 18*) as a form of *Chlamydomonas pulvisculus* Ehrenb. Golenkin also appears to have had this species in Russia, and to have confused it with another genus, for one of his figures (**5**, *f. 19*), described as a reduced form of *Pteromonas alata* (Cohn) Seligo, can hardly be anything else than a young cell of *L. Francei*. Apparently the species has not been studied or scarcely even reported otherwise, except by Dangeard. In 1902 Chodat (**2**) transferred to the newly founded genus his species *Chlamydomonas stellata*, briefly described six years before (**1**); he even appears to have been doubtful of the distinctness of his form from Dangeard's type, though both species have been accepted by West (**8**, p. 172) and Wille (**9**, p. 19), who have reproduced the original illustrations.

The genus presents a cell organization almost precisely like that of *Chlamydomonas*, probably its nearest relative, with the exception that its outer wall is furnished with variable irregularities or protuberances, which in the type species are frequently more developed on the posterior part of the cell, while in *L. stellata* the more uniformly triangular lobes are figured as covering the wall nearly to the region of insertion of the cilia. It

[The BULLETIN for April (**49**: 75-122. *pl. 3, 4*) was issued May 18, 1922.]

is probable that *Lobomonas* has escaped the notice of collectors to some extent because of the minute size of the cells, but doubtless it is actually one of the rarest genera of the *Chlamydomonas* group. The two new species now presented serve to emphasize the unity and distinctness of the genus, and also provide certain features of division and conjugation not known hitherto, which indicate a fundamental parallelism with *Chlamydomonas*.

Lobomonas pentagonia sp. nov.

This species, the first of the genus to be reported in England, I believe, was discovered in considerable abundance, together with two species of *Pteromonas*, at Ham Common, Surrey, near Kew, in 1920. The habitat was the border of a small shallow pond at the west end of the common, a place frequented by cows and horses, and therefore supplied with water containing a considerable amount of nitrogenous organic matter in solution: in fact the general conditions were very like those of the much smaller pool where *Lobomonas rostrata*, to be described presently, was found with another species of *Pteromonas* in New Jersey.

Like all other species of the genus, *L. pentagonia* is very minute, but it is more constant in form than *L. Francei* or *L. rostrata*. When seen in side view the cell appears rather pentagonal in outline (FIGS. 1–4), but careful focussing shows that the angles do not all lie in the same plane. Polar views often show five to eight protuberances (FIG. 14), likewise not all at the same level. One of the most symmetrical specimens, when resting with its ciliated end turned upward, shows four anterior protuberances and, alternating with them, four others at the posterior end of the zoospore (FIG. 5); the number, however, is variable. The protoplast, including the chromatophore, in young individuals usually extends into and fills the protuberances, and ends anteriorly in a somewhat obtuse beak, to which the two cilia are attached (FIG. 1). In older specimens the protoplast usually retracts from one or more of the wall protuberances and leaves them empty: they do not appear like dense gelatinous structures. The chromatophore is more or less hollowed out in the common *Chlamydomonas* fashion but thickened in the region where the pyrenoid lies in a somewhat lateral position. The two alternately pulsating vacuoles lie in a plane nearly perpendicular to that passing through the two extended cilia (FIG. 5), as in most species of *Chlamydomonas*, so that in the ordinary face view of the cell only one is usually seen. The

narrow rod-shaped red eye-spot lies in or just beneath the plasma membrane slightly in front of the middle of the cell. Its position with relation to the cilia is more like that which it occupies in *Brachiomonas* than that in *Chlamydomonas*, as brought out recently by the writer (**6**), though the dorsiventral differentiation here is perhaps less constant and definite than in the two related genera.

ASEXUAL REPRODUCTION. Dangeard (**3**) reports that his attempts to cultivate *L. Francei* in a moist chamber did not succeed, and that it was difficult to obtain the multiplication of the organism. He shows that the cells come to rest and generally become rounded in shape, then divide into four or eight daughter cells which escape as zoospores. He gives no figure to support Wille's (**8**) surmise that division is longitudinal. In our two new species I found that very generally after motile cells were mounted in a hanging drop they would for the most part come to rest in a few hours and proceed to divide, though in many cases the daughter cells failed to become motile or escape. In both species pyrenoids were not seen in any dividing specimens until the daughter cells had begun to take on the typical form, so that it would appear necessary to conclude that in this genus, as in *Brachiomonas* and in some species of *Chlamydomonas*, the pyrenoid disappears before the first cleavage, and that one is formed *de novo* in each daughter cell.

In *L. pentagonia* the first division plane usually appears at first sight to be transverse to the longitudinal axis of the cell, but several cases were observed which lead to the conviction that there is regularly a rotation of the protoplast during or before the beginning of cleavage. FIGS. 6 and 7 show two stages of division where the protoplast has revolved to an oblique position when the cleavage begins; probably the rotation was delayed more than usual in this case; here the original contractile vacuoles persist after the division of the nucleus. Fig. 8 shows a case where what I am sure the original vacuoles persisted until the end of cleavage into two daughter cells. In case of the formation of four zoospores the second plane of cleavage is perpendicular to the first, *i. e.* it lies in a longitudinal axis of the mother cell: it may lie in a single plane through the two halves (FIG. 11), or the second division plane in one half cell may be perpendicular to that in the other (FIG. 12).

SEXUAL REPRODUCTION apparently has not been observed hitherto in this genus. I considered it good fortune, therefore, to discover three or four cases of conjugation taking place almost simultaneously in one hanging drop. The gametes have the general form and character of the vegetative cells, but are much smaller, provided with an excessively delicate cell wall, and the cilia are longer than the cell body. In the first case seen, one gamete was rather broad and pillow-shaped, with a distinctly visible cell wall, while the other was narrower and probably more nearly cylindrical, and furnished with a wall so delicate that it was detected only in its subsequent behavior. The two gametes became engaged by their cilia, but not otherwise in contact, and remained in this position for at least a half hour, with slight dancing movement (FIG. 15); the cilia, most if not all of this time, were trailed backward along the sides of the narrower gamete. The first movement toward joining was in a sudden break of the anterior papilla of the broad gamete, whereby a broader papilla of colorless cytoplasm surged forward and presently plastered itself on the beak of the unchanged gamete (FIG. 16), the remainder of the protoplast of the broader gamete then distinctly withdrawing from the posterior part of its wall (FIG. 17). Now for a period of about a half hour the remainder of the protoplast of the broader gamete was gradually oozing out of its wall and into the narrower gamete: even yet the narrower gamete hardly showed a wall, but it seemed evident that one must be present, since the posterior part of this gamete rigidly retained its original form (FIGS. 19, 20). After this point more active ciliary movement carried the zygote beyond possibility of observation.

A second case showed a similar figure of the narrow gamete remaining rigid for as long a time as it could be followed. In all probability this wall of the narrow gamete is finally thrown off separately, permitting the rounding up of the plasmatic mass to form a spherical zygospore. A third case showed the gametes more nearly equal, and it was clear that the walls of both were practically alike in character and not easily abandoned (FIG. 21), so that fusion was long delayed.

There is in this species apparently little differentiation between the gametes; indeed one might be inclined to regard the difference in size as merely accidental. Nevertheless from the behavior of the cilia, that is, both pairs for the most of the time stretching back alongside the narrower gamete, one may assume

a certain degree of differentiation. The conjugation of this species presents a close parallel to that described by Goroschankin for *Chlamydomonas reticulata* (**5**, p. 126, *pl. 3, f. 6–8*). He states that the gametes show little difference in size, and that they sometimes simultaneously slip out of their walls; but more frequently, after the beginning of conjugation, one of the gametes first throws off its wall and takes on a globose form, then the second does likewise, and then the two rounded masses go on to complete fusion.

The subjoined Latin diagnosis presents the chief characteristics of this species:

Lobomonas pentagonia sp. nov. *L.* cellulis vegetativis minutis, membrana a latere aspectata forma aliquanto pentagonia sed angulis rotundatis (verrucis) haud omnibus in eodem plano a vertice aspectata rotundata cum 5–8 verrucis, aliis anterioribus, aliis posterioribus protoplasto vel membranae conformali vel plus minus contracto et ellipsoideo, cum rostello conico ad quod cilia bina cellulae longitudinem fere adequantia affiguntur; chromatophoro excavato, pyrenoidem unum sublateralem portante, et in parte excavata nucleum lateralem includente; stigmate bacilliformi paululum ante mediam cellulam sito; vacuolis contractilibus binis in rostello cytoplasmatico positis.

Propagatio fit 2 aut 4 zsooporis intra cellulae matricalis membranam ortis, divisione priore visa quasi transversaria propter protoplasti rotationem sed vero longitudinali.

Generatio fit gametis parvulis, vel subaequalibus vel aliquanto disparibus, membrana tenuissima vestitis, inter se binatim copulantibus.

Longit. cell. veg. 10–13 μ; lat. 9–10 μ. Longit. gametarum ca. 8 μ; lat. 4–5 μ; longit. ciliorum ca. 13 μ.

Hab. in stagni margine. Ham Common, Surrey, England, 1–7 Aug. 1920.

Lobomonas rostrata sp. nov.

This form, the first representative of the genus to be reported in America, at first sight appeared very similar to *L. Francei* Dangeard (**3**, p. 115), but careful study disclosed differences as important as those which distinguish most species of *Chlamydomonas*, so that I feel obliged to regard it as a new species. I first found a few individuals in examining a collection of *Gonium pectorale* and an undetermined species of *Chlamydomonas*, obtained the last of September, 1919, from a rain-water pool of a highway in the southern part of Englewood, New Jersey. Later it was interesting to discover that the species had been collect-

ed about a week earlier in a much deeper pool, about half a mile distant from that just mentioned; this discovery was due to the fact that a fine colony of the *Lobomonas* developed on an agar plate containing a sample of my first collection of *Pteromonas* from this pool. The new species continued to appear sporadically in later gatherings from the same pool, the last being made November 12; it was also collected in October, together with *Chlamydomonas metastigma* Stein, from another rain-water pool in a wheel-rut, not far from the one first mentioned, though separated from it by railroad tracks bordered by a deep ditch on either side. The first mentioned wheel-rut yielded a few individuals in the following season. A few specimens of this species were also discovered during the past summer in a collection from a similar wheel-rut in northern Vermont: here it was accompanied by *Gonium pectorale*, *Pandorina*, *Chlorogonium*, *Chlamydomonas*, and a very interesting new form of *Polyblepharides*, to be described in a forthcoming paper. The *Lobomonas* never appeared to be abundant like its associates in the same pools; usually not more than a dozen or two specimens turned up in one hanging drop mount.

The vegetative cells or zoospores of this species most commonly have a somewhat obpyriform shape (FIG. 22–27) though they are sometimes almost ellipsoid. In younger individuals the cell wall is so delicate and close-lying as to be indistinguishable for the most part, but in older cells it is well developed (FIGS. 28, 29); it is generally produced into a variable number of lobes, of which from five to seven or sometimes as many as ten appear in a face view; that these lobes are developed on all sides of the cell is clearly shown in a polar view (FIG. 30). At the anterior, usually broader end, the wall is extended into a truncate, wedge-shaped beak, or possibly more typically this takes the form of a more or less double papilla (FIG. 33); on account of the minute size of the organism it is often most difficult to see clearly the exact structure of this protuberance, which is one of the most characteristic features distinguishing this species from the two hitherto described in Europe. Sometimes the wall appears to be uniformly thin, sometimes thickened at the end of the lobes, and sometimes considerably thickened throughout. The protoplast, indistinguishable outwardly from the bright green chromatophore, fills the lobes in young individuals; in older cells it retracts more or less, so as to leave some or all of the lobes colorless. In such cases it is not easy to determine whether the

lobe is a dense, gelatinous structure, or simply membranous and separated by a space from the protoplast. In certain cases the latter interpretation is clearly indicated, for the tip of the lobe is manifestly of thickened grayish wall substance, with a clear space inside (FIG. 37). The cilia are attached at a single point to the anterior end of the protoplast, which is usually obtuse, though it may have a slight beak; they immediately diverge at a wide angle to pass separately through the papilla of the wall, and are often seen in quiescent individuals stretching out stiffly in the form of a v; their length is as variable as the cell outline, often being less than the cell length, but perhaps more characteristically distinctly greater than the cell length. At the base of the cilia are the alternately pulsating vacuoles, lying regularly in such a position that a line passing through the two is perpendicular to the plane in which the quiescent cilia lie, so that only one of the vacuoles is seen when both cilia are equally clear, but both may appear at the same level when one of the cilia is behind the other (FIG. 29). The single pyrenoid occupies a lateral position in the deeply hollowed out chromatophore (FIGS. 24, 26), contrasting sharply with the axial pyrenoid in a massive chromatophore described and figured by Dangeard (3) in *Lobomonas Francei*. The small rod-shaped red eye-spot lies in front of the middle of the cell, but apparently not in a constant position with reference to planes passing through the cilia and contractile vacuoles, as is the rule in *Pteromonas* and in many species of *Chlamydomonas*.

REPRODUCTION. The earliest stages of division found presented the appearance of a cleavage transverse to the longitudinal axis of the cell. More careful consideration, however, here, as in *L. pentagonia*, indicates that an early rotation of the protoplast has eluded observation, for in FIG. 36 two contractile vacuoles, lying in what appears to be the original colorless anterior cytoplasm, now appear on the side of the cell. Even in such a case as that shown in FIG. 37, there is a colorless central region which can only be explained on the supposition that the anterior end of the protoplast had revolved ninety degrees from its original position, here not clockwise as in FIG. 36, but in a vertical plane with reference to the observer. The mother cell retains very much of its original form throughout the process of division, instead of rounding up, which Dangeard describes as being the general rule for *L. Francei*. Here also there may be four or eight daughter cells formed, and they regularly show the

typical obpyriform and lobed shape, and sometimes even show the protoplast somewhat separated from the new cell wall, before escaping from the mother cell. The escape appears to be accomplished by a gradual softening and disintegration of the wall of the mother cell, rather than by rupture at a single point (FIG. 40). The eight daughter cells of this figure are so small as to occasion the surmise that they might be gametes, but conjugation was not seen in this species.

The chief characteristics distinguishing this species from *L. Francei* Dang. are: the general obpyriform shape, the well developed anterior beak or papilla, the lateral pyrenoid, and the persistence of the form of the mother cell during division. The description may be summarized as follows:

Lobomonas rostrata sp. nov. *L.* cellulis vegetativis plus minusve obpiriformibus, rarius ellipsoideis; membrana cellulae in verrucas plures quarum 5–7 vel etiam 10 in facie una apparent producta, atque in polo anteriore rostello cuneiformi seu papilla subduplici instructa, per quod rostellum procurrunt cilia bina longitudine corpus cellulae adaequantia vel longiora, vel breviora: protoplasto primum membranae verrucas complente, deinde plus minus contracto et ellipsoideo: chromatophoro valde excavato, pyrenoidem unum lateralem portante: stigmate bacilliformi, paullulum ante mediam cellulam sito: nucleo majore nunc paene centrali, nunc laterali, rarius posteriori; vacuolis contractilibus binis juxta papillam anteriorem suppositis.

Propagatio fit protoplasto cellulae vegetativae jam immobilis diviso in 4 aut 8 zoosporas, quae formam typicam priusquam evaderunt ex cellulae matricalis membrana adipiscuntur. Copulatio haud observata.

Longit, cell. veg. 5–12 μ; lat. 4–8 μ; long. ciliorum ca. 5–14 μ.

Hab. in aqua pluviali quae colligitur in viis terrenis, et in lacuna quadem lutulenta in pascuo pecuario. Englewood, New Jersey, Sept.–Nov. 1919, Sept. 1920: Shelburne, Vermont, 3 Aug. 1921.

It has been already pointed out elsewhere (**6**) that *Lobomonas* is to be regarded as a special offshoot from *Chlamydomonas*, not leading to any higher group so far as we know at present. It might be thought simple to derive the genus directly from the Polyblepharidaceae, even from the genus *Dunaliella*, which clearly appears to be the immediate ancestor of *Chlamydomonas*, since it has all the features of cell organization of the latter genus except for the lack of a firm cell wall. When, however, it is recalled that the gametes of *Lobomonas*, reported above for the first time, possess cell walls, it will be more natural to look for

its ancestry among those species of *Chlamydomonas* which posses walled gametes, and are therefore ranked as the primitive members of the genus, since their vegetative cells and gametes differ (visibly) only in point of size. Our two new species of *Lobomonas*, moreover, also resemble a number of the relatively primitive members of *Chlamydomonas* in their method of cell division, namely through a cleavage which is fundamentally longitudinal but early shifts to a transverse position. The question then arises, what influences led to the divergence of cell form, which is practically the sole basis of separation between the species forming the small genus *Lobomonas* and the much larger number comprised in *Chlamydomonas*.

A CONSIDERATION OF MORPHOGENESIS IN PRIMITIVE ALGAE

This whole problem of the origin and inheritance of cell form in primitive organisms is one of very great interest which has received comparatively little attention. Perhaps the most extended discussion of the question has been furnished by D'Arcy Thompson (**22**), who regards surface tension as the paramount factor in the determination of cell form. Though at one point he admits that 'the physical cause of the localized inequalities of surface tension remains unknown', and at other times hints that an internal chemical heterogeneity may have some influence in connection with such differences in surface tension, nevertheless again and again he reiterates his main thesis in regard to unicellular organisms, 'that not only their general configuration but also *their departures from symmetry* may be correlated with the molecular forces manifested in their fluid or semi-fluid surfaces'. This explanation seems to us entirely inadequate and not in harmony with the general weight of evidence. For the particular organisms considered here and in the previous paper on *Brachiomonas* (**6**) we can offer little direct evidence; but there are certain facts which suggest that the conception of the non-homogeneity of the protoplasmic structure of the cell, as developed by Rhumbler (**19**) and Harper (**12**) supplies a much more workable hypothesis than the idea of mere surface tension forces.

Passing over Rhumbler's work on protozoa, the most thorough treatment of morphogenesis within a small group of primitive plants is found in the studies of Harper (**11, 12**) on *Pediastrum*. He believes that the general four-lobed form

of the cells familiar in most species of *Pediastrum* may well have arisen in evolution as a consequence of the pressure and contact relations of the young cells in the sixteen-celled colony, regarding them merely as surface tension globules: nevertheless he has shown repeatedly that this four-lobed form does not depend in ontogeny upon the forces which may have been responsible for it originally, but that it is inherited and may reach full expression when there is the least possible contact with other cells of the colony. Repeatedly Harper calls attention to the view that though surface tension is commonly acting as a morphogenetic factor, nevertheless 'it is the inherited anomogenous consistency of the cells which is of most significance in determining their form.' In strictly unicellular organisms like *Lobomonas* and *Brachiomonas*, there is an absence of the interaction of contact and pressure stimuli which are important influences in the variation of the *Pediastrum* colony; nevertheless in the fundamental organization of the cell the factors must be parallel in the main. In both cases the lobed form may be regarded as adaptive for the general metabolism of the cell. In *Pediastrum* the development of spines is usually looked upon as a case of primitive differentiation for protection, and in *Lobomonas* and *Brachiomonas* the lobes might easily be conceived of as subserving a similar function: in point of fact, I have observed that when these forms are found in the same pools with smooth-walled ovoid *Chlamydomonas* cells, it is the latter that are devoured by protozoa, while they rarely or never prey upon the lobed forms, even though the latter are smaller. However, when two species of *Chlamydomonas* are present together, sometimes one is rapidly consumed by protozoa while the other is ignored. The anti-selectionist, moreover, might fairly inquire why it is that these genera of bizarre form have produced very few species, in comparison with the extraordinarily successful genus *Chlamydomonas*, which has attained well nigh three score species, so far as taxonomy goes, in recent years.

Wille (**9**, p. 19) ascribed to the zoospores of *Lobomonas* the characteristic of 'deutliche Metabolie.' I cannot find that Dangeard uses this term in connection with this genus; but as defined by him elsewhere* as amoeboid movement, or used

*On désigne sous le nom de métabolie une sorte de mouvement par contraction du corps particulier à quelques Euglènes, Amibes, Monades, etc. C'est ce que nous appelons mouvement amiboïde. [Dangeard: Recherches sur les algues inférieures. Ann. Sci. Nat. Bot. VII. **7**: 144. 1888.]

more exactly by other recent writers (especially in connection with the Polyblepharidaceae) in the sense of euglenoid or amoeboid change of form—and this was the usage of Perty*, by whom the word appears to have been coined in 1852—the term is misleading when applied to *Lobomonas*: or at least it can be used only in a very restricted sense in connection with this genus. The young cells of *Lobomonas* of course do undergo a certain change of outline during the formative process within the wall of the mother cell: ordinarily essentially the mature form is acquired and fixed before their escape, and I have found no evidence that it is appreciably altered afterward during activity, though, in appearance only, the mature cell may be distinctly reminiscent of *Amoeba*. Nevertheless, this idea of amoeboid change of form is most suggestive in a discussion of the formative period of such genera as we have under consideration, and for this restricted period I believe we are entirely justified in drawing a parallel with the results of certain recent researches on the production of pseudopodia.

A brief survey of this work may be useful in this connection. McClendon (**16**) has attempted to explain amoeboid movement as due to local increase in permeability, the *Amoeba* simply receding from the side on which the permeability has been increased. Its author himself admits the difficulty of explaining positive reactions by this theory, and it certainly does not offer any sufficient explanation for the assumption of the characteristic cell-form shown by our developing chlamydomonads. The closely related hypothesis that production of pseudopodia may be accounted for by local variation in surface tension has been widely invoked. The re-statement of this theory lately made by Thompson (**22**) may here be passed over, even as this stimulating writer has all but ignored the evidence which has been accumulating against the surface tension explanation. Both the permeability idea and the surface tension explanation as ordinarily employed are objectionable, in that they depend too

*Metabolie. Hirunter verstehe ich die durch *innere Vorgänge* bedingte wechselnde Gestaltänderung. Seit langem bei den Amiben bekannt ist sie bei den Infusorien so viel als nicht beachtet worden. [Perty: Zur Kenntniss kleinster Lebensformen, p. 127. Berne. 1852.]

Since this term Metabolie seems to be unfamiliar to American botanists because of its very restricted usage, and since it has even been rendered as equivalent to metabolism in a recent German-English dictionary for chemists, it appears to be worth while to call attention to this original definition.

much upon external environmental influences to account for the requisite local variability, though this element is not necessarily involved in either theory.

The beginning of the more recent undermining of the surface tension explanation of form change is found in the work of Jennings (**14**), who from painstaking direct observation reported that the currents in a moving *Amoeba* as a whole 'are not similar to those of a drop of inorganic fluid that is moving or elongating as a result of a local increase or decrease in surface tension', and in particular that 'the movements of material in a forming pseudopodium are not like those in a projection which is produced in a drop of inorganic fluid as a result of a local decrease in surface tension'. From these observations Jennings was forced to the conclusion 'that changes in the surface tension of the body are not the primary factors in the movements and reactions of *Amoeba*'. Similar conclusions from direct observation were announced two years later by Dellinger (**10**), whose clever photographs of *Amoeba* viewed from the side reveal the locomotion of the organism as a sort of 'walking,' rather than a flowing of a fluid substance upon the substratum. These negatory conclusions have been reinforced and extended by a series of recent researches in the field of microdissection (**15**, **21**, **13**). From these there is general agreement that the structure of *Amoeba* (and probably of many other rhizopods and cells of primitive organization) is not of the nature of a simple fluid mass governed chiefly by surface tension forces, but rather that it is a highly non-homogeneous system, consisting of comparatively fluid endoplasm surrounded by an ectoplasm which has often the character of a semi-rigid gel, possessing a considerable elasticity, though the two regions may very probably grade into one another imperceptibly.

Finally, the experiments of Hyman (**13**) reveal in each pseudopodium of *Amoeba* a gradient in susceptibility to potassium cyanide, the susceptibility being greatest at the distal end and decreasing proximally. This susceptibility gradient is regarded as being a metabolic gradient which arises before the pseudopodium appears, 'and hence the metabolic change which produces increased susceptibility is the primary cause of pseudopodium formation.' Liquefaction or solation is regarded as the cause of the extension of a pseudopodium, and coagulation or gelation as the cause of its retraction: the liquefaction is believed to be brought about by the metabolic change just re-

ferred to. This theory that amoeboid movemnt is due to alterations of the colloidal state is only in the nature of confirmation and extension of the view advanced more than forty years ago by Montgomery (**17, 18**) that protoplasmic movement of amoeboid organisms consists in 'an alternate expansion and contraction of organic substance': Montgomery even anticipated Hyman in expressing the idea that the liquefaction which occasions pseudopodium advancement is itself due to metabolic changes, while he anticipated Rhumbler (**19**) in the idea of a non-homogeneity of the primitive protoplasmic mass which permits various functions to be carried on in different regions at the same time.

This somewhat lengthy excursus (which is yet only the briefest possible summary of a voluminous literature) has been introduced here only to bring before botanists, to whom the field may be unfamiliar, facts which it is believed may be directly applied in the case of the chlamydomonads we are considering. The form development of *Lobomonas*, *Brachiomonas*, and *Pteromonas* must be essentially amoeboid for a brief period during the organization of the daughter cells, and we are justified in assuming that their lobes and excrescences are the expression of the same non-homogeneous organization of the protoplast as is characteristic of *Amoeba*.

For this view, furthermore, we may draw an additional parallel from the results of microdissection. In the developing oogonium of *Fucus*, Seifriz reports (**21**) that the viscosity of the protoplasm changes from liquid consistency in the young uninucleate stage to slightly viscous consistency when the division into eight eggs is just complete, and to decidedly viscous consistency (just under the viscosity of glycerine) in the mature normally discharged egg: that is, in Seifriz's scale of ten grades of viscosity—the first attempt on the part of microdissectionists at standardization in this matter—the variation is from grade 3 to grade 6. Yet further, from the behavior of disintegrating eggs of *Fucus*, Seifriz (**20**) finds that the process may be localized in such a manner as to indicate 'a gross structure of the egg plasm, *i.e.*, the protoplasm is composed of many centers of activity in which different chemical reactions take place.' I have recently found a condition almost precisely similar in the case of a newly discovered polyblepharid genus which it is hoped may soon be published. The cells of this species, though surrounded only by an exceedingly delicate protoplasmic membrane, are never-

theless able to maintain for extended periods an elaborately eight-ridged or winged prismatic form, and in disintegration often break only at one or two points, thus permitting the greater body of the protoplasm to remain practically intact, while only small streams ooze out. From these observations we are justified in concluding that such cells as those of *Brachiomonas* and *Lobomonas*, could we apply methods of microdissection, would be found to have protoplasm of a comparatively fluid consistency during division, but that local increase in viscosity gradually permits the fixation of the characteristic lobed form of the cell. When it is recalled that in these two genera the pyrenoids regularly disappear in preparation for cell division, and are reorganized with the maturing of the daughter cells, it will readily be seen that in this reorganization, combined with the ordinary processes involved in division of cells inheriting differentiation of polarity in at least three axes or planes, there is abundant room for the play of such metabolic changes as might well account for considerable differences in viscosity in different parts of the developing daughter protoplasts. It is this non-homogeneity of structure, involving very likely chemical as well as physical differences, which may be regarded as the dominant factor in the determination of form in such organisms. From this standpoint, the problem as to how this characteristic form may be transmitted in heredity does not seem so insoluble as it does on the assumption of form determining unit factors in a germ plasm.

One further point may be emphasized. It is stated by Thompson (**22**) that when 'owing to some heterogeneity of the substance' the operation of uniform surface tension forces is modified so as to result in the production of the ellipsoid cell characteristic of yeast, for example, 'this or any other asymmetrical form, once acquired, may be retained by virtue of the solidification and consequent rigidity of the membranous wall of the cell.' In the case of the organisms with which we are here concerned at least, I am confident, the development of the cell wall is not a necessary condition of the maintenance of specific form; for the new polyblepharid mentioned above, and others of the same group, as well as the gametes of *Brachiomonas*, are able to preserve essentially the same form for long periods, in spite of the fact that they are clothed only with a protoplasmic membrane of such excessive thinness that it is practically undemonstrable. It is then, owing to relative viscosity in their

protoplasmic substance that these motile organisms are able to attain and maintain their specific form.

In both *Brachiomonas* and *Lobomonas* we have noted that not infrequently mature cells exhibit a more or less rounded form of the protoplast inside of the cell wall, while the latter maintains the typical lobed form as fixed in the formative period. Such conditions are not improbably produced by shrinkage due to loss of a certan amount of water from the protoplast, accompanied by a tendency to decrease in viscosity of the outer layer, in which case, surface tension would tend to bring about a more rounded form. In other words, the maturing protoplast might be said to show a tendency to revert to what might be considered the ancestral form in preparation for reproduction.

It is a pleasure to acknowledge my debt to Professor R. A. Harper for numerous stimulating discussions of problems connected with morphogensis, and for reading this paper in manuscript.

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LITERATURE CITED

A. In connection with *Lobomonas*

1. **Chodat, R.** Matériaux pour servir à l'histoire des Protococcoidées V. Bull. Herb. Boiss. **4**: 273–280. 1896.
2. ——Algues vertes de la Suisse. Berne. 1902.
3. **Dangeard, P. A.** Mémoire sur les Chlamydomonadinées ou l'histoire d'une cellule. Le Botaniste **6**: 65–292. *f. 1–20.* 1899.
4. **Golenkin, M.** *Pteromonas alata* Cohn. Bull. Soc. Imp. Nat. Moscou **5**: 417–430. *pl. 11.* 1891.
5. **Goroschankin, I. N.** Beiträge zur Kenntniss der Morphologie und Systematik der Chlamydomonaden. Bull. Soc. Imp. Nat. Moscou **5**: 101–142. *pl. 1–3.* 1891.
6. **Hazen, T. E.** The phylogeny of the genus *Brachiomonas*. Bull. Torrey Club **49**: 75-92. *pl. 3, 4.* 1922.
7. **Stein, F.** Der Organismus der Infusionsthiere **3**[1]. Leipzig. 1878.
8. **West, G. S.** Cambridge Botanical Handbooks. Algae **1**. Cambridge. 1916.
9. **Wille, N.** Chlorophyceae. Engler & Prantl, Nat. Pflanzenfam **1**[2], Nachtr. 1911.

B. On the problem of morphogenesis

10. **Dellinger, O. P.** Locomotion of *Amoebae* and allied forms. Jour. Exp. Zoöl. **3**: 337–358. *pl. 1, 2 + f. 1-27.* 1906.
11. **Harper, R. A.** The evolution of cell types and contact and pressure responses in *Pediastrum*. Mem. Torrey Club **17**: 210–240. *f. 1-27.* 1918.
12. ——Organization, reproduction, and inheritance in *Pediastrum*. Proc. Am. Phil. Soc. **57**: 375–439. *pl. 5, 6 + f. 1–35.* 1918.
13. **Hyman, L. H.** Metabolic gradients in *Amoeba* and their relation to the mechanism of amoeboid movement. Jour. Exp. Zöol. **24**: 55–99. *f. 1-14.* 1917.
14. **Jennings, H. S.** Contributions to the study of the behavior of lower organisms. The movements and reactions of *Amoeba*. Carnegie Inst. Washington Publ. 16: 131–234. *f. 30–78.* 1904.
15. **Kite, G. L.** Studies on the physical properties of protoplasm. I. The physical properties of protoplasm of

certain animal and plant cells. Am. Jour. Physiol. **32**: 146–164. 1913.

16. **McClendon, J. F.** Ameboid motion and tropisms. Physical chemistry of vital phenomena, pp. 148–156. Princeton. 1917.

17. **Montogomery, E.** The elementary functions and the primitive organization of protoplasm. St. Thom. Hosp. Rep. **9**: 75–100. 1879.

18. ——Zur Lehre von der Muskelcontraktion. II. Die amöboide Bewegung. Arch. Gesam. Physiol. **25**: 499–509. *pl. 9*. 1881.

19. **Rhumbler, L.** Der Aggregatzustand und die physikalischen Besonderheiten des lebenden Zellinhaltes. Zeits. Allg. Physiol. **1**: 279–388. 1902.

20. **Seifriz, W.** Observations on the structure of protoplasm by aid of microdissection. Biol. Bull. **34**: 307–324. *f. 1-3*. 1918.

21. ——Viscosity values of protoplasm as determined by microdissection. Bot. Gaz. **70**: 360–386. 1920.

22. **Thompson, D'Arcy W.** On growth and form. Cambridge. 1917.

Explanation of plates 5 and 6

Figures drawn with camera lucida from living material kept in hanging drops (VanTieghem cells of standard height of 5 mm.): Leitz compens. oc. 12 was used in combination with oil immers. obj. 1-12 inch, or Spencer 2 mm. The drawings have been reduced one half in reproduction, making the present magnification approximately 1150 diameters for FIGS. 1–21 and 41, and 1375 diameters for FIGS. 22–40.

PLATE 5

LOBOMONAS PENTAGONIA Hazen

FIGS. 1–5. Typical vegetative cells or zoospores: in FIGS. 1–3 the stigma lies on the under side of the cell.

FIG. 5. Anterior polar view: four anterior lobes emtpy, chromatophore filling four posterior lobes.

FIG. 6. Protoplast rotating clockwise in preparation for division; 7 P. M.

FIG. 7. The same cell at 7:05 P. M; beginning of cleavage.

FIG. 8. Division into two zoospores completed at 6:30 P. M.

FIG. 9. Another individual: pyrenoid and cilia beginning to appear in daughter cells; nucleus in most advanced lobe: 10:30 P. M.

FIG. 10. Pentagonal form attained by daughter cells.

FIG. 11. Four daughter cells in one plane.

FIG. 12. Two daughter cells with axes perpendicular to those of the other pair.

FIG. 13. An unusually simple form: cilia contracted into a ball.

FIG. 14. Cell in posterior polar view.

FIGS. 15–20. Stages in conjugation of a pair of slightly unequal gametes: FIG. 15 at 1:45 P. M.; FIG. 16 at 2:15; FIG. 17 at 2:16; FIG. 18 at 2:25; FIG. 19 at 2:40; Fig. 20 at 2:45.

FIG. 21. Zygote formed by conjugation of equal walled gametes.

PLATE 6

LOBOMONAS ROSTRATA Hazen

FIGS. 22–27. Typical young vegetative cells.

FIGS. 28, 29. Mature cells of less common form, but with well developed wall, FIG. 29 showing edge view of beak.

FIG. 30. Anterior polar view.

FIGS. 31, 32. Cells showing persistence of form some time after loss of motility.

FIG. 33. Relatively large mature cell, pyrenoid and stigma underneath.

FIG. 34. The same cell 24 hours later: four daughter cells completely organized except for cilia, 11 P. M.

FIG. 35. One of the four daughter cells, one day later, not very well formed, probably because of unfavorable conditions.

FIG. 36. Beginning of cleavage, after clockwise rotation of protoplast; 9:30 P. M.

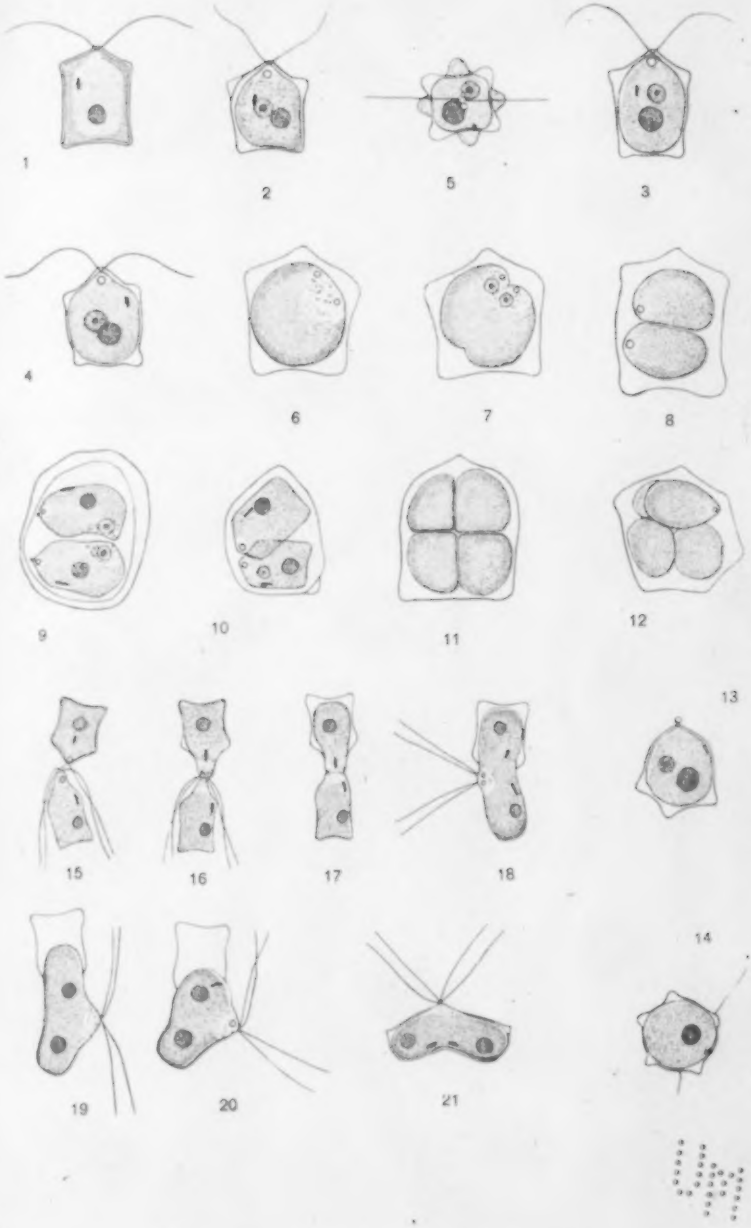
FIG. 37. Similar division, after rotation of protoplast in vertical plane; 10:30 P. M.

FIG. 38. Second cleavage just completed; 10:30 P. M.

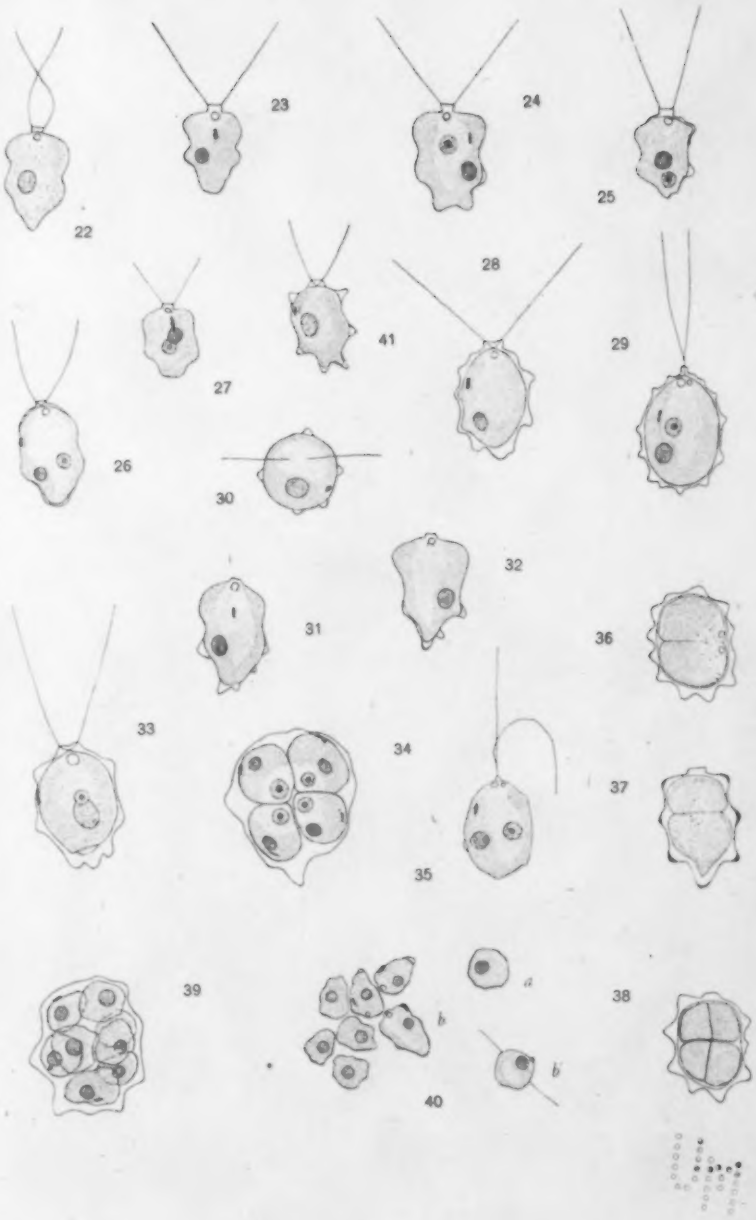
FIG. 39. Eight daughter cells (perhaps gametes) 6 P. M.

FIG. 40. The same at 9:30 P. M.: daughter cells held by gelatinized wall of mother cell: cell *a* moved out sluggishly at 8:30; at 10 P. M. cell *b* backed out and presently rested on end, cilia downward as at b^1.

FIG. 41. Mature cell from Shelburne, Vermont, August 3, 1921. All other figures from New Jersey material, in 1919.



LOBOMONAS PENTAGONIA HAZEN



LOBOMONAS ROSTRATA HAZEN

The development of the flower and embryogeny of Martynia louisiana

FLORA ANDERSON.

(WITH PLATES 7 AND 8 AND TWENTY-FIVE TEXT FIGURES)

INTRODUCTION

The most common and widely distributed representative of the Martyniaceae in temperate North America is *Martynia louisiana* Mill. Although the literature on the family is chiefly taxonomic, the descriptions are meagre and confusing. All the species have, at some time, been placed in the genus *Martynia*. The ten or more known species comprise three genera, native to the warmer parts of the western hemisphere.

Efforts were made to secure seeds and to grow plants of the different species for comparison, in order, if possible, to work out the taxonomy of the family. Seeds were obtained from seed-houses both in the United States and in England and also from the Bureau of Plant Industry, the University of Texas and the Mississippi Agricultural College.

From seeds secured through the Bureau of Plant Industry, quite a number of plants of *Martynia louisiana* were grown—all the plants producing viable seeds—and one specimen of *Martynia lutea* Lindl. which, although maturing seemingly normal fruit from selfed flowers, produced no viable seeds. Reciprocal crosses of *Martynia lutea* and *Martynia louisiana*, and of *Martynia lutea* and *Martynia fragrans* Lindl. failed.

From seeds furnished by seed-houses, the University of Texas and the Mississippi Agricultural College, quite a number of plants of *Martynia louisiana* and *Martynia fragrans* were grown in Montgomery County, Indiana, during the summers 1915–1919. The two species mentioned above cross very readily, producing in all cases viable seeds. These plants, grown in the open in rich soil and under practically the same conditions, showed very few differences except in the color of the corolla, which is more or less a variable character. The similarity of the plants seems to indicate that they belong to the same species, but more cultures must be studied before this point can be definitely determined.

In as much as no morphological work seemed to have been done on this family, a study of *Martynia louisiana* and *Martynia fragrans* was undertaken, the results of which are given in the following pages. While the study was based mainly on *Martynia louisiana* no structural differences between the two species were observed.

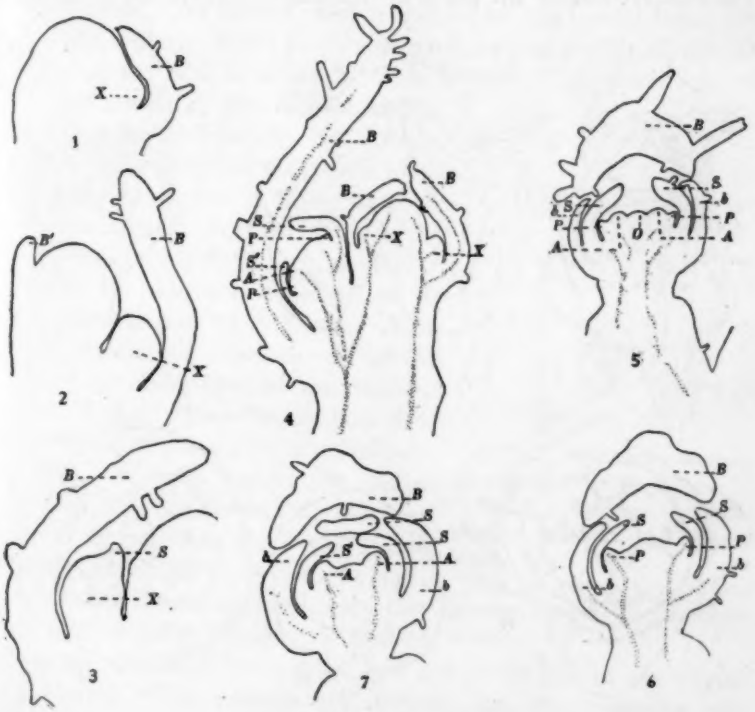
MATERIAL AND METHODS

The material used for this study was collected from plants of *Martynia louisiana* and *Martynia fragrans* grown in the field, in Montgomery County, Indiana. Collections were usually made during the month of August, when the plants were most vigorous. The apices of racemes, small flowers and stamens, pistils and young fruits in various stages of development were killed and fixed in a 1 per cent chromo-acetic acid or in chrom-osmic-acetic acid one to two hours and then in chromo-acetic acid twenty-four to thirty-six hours, washed, dehydrated, and embedded through chloroform. To determine the time necessary for the pollen tube to reach the egg, pollination was controlled, and, beginning at one hour after the application of the pollen, collections were made at intervals of one hour for fourteen consecutive hours. These collections were of whole pistils which were killed and fixed in chrom-osmic-acetic acid one to two hours and then in chromo-acetic acid thirty-six hours. Beginning thirty hours after pollination, collections of pistils and young fruits were made at intervals of six hours for two hundred and four hours. Sections were cut 4–10 μ, most of them 5 μ thick; those of whole pistils were longitudinal and 4–5 μ in thickness. Both modified triple and Heidenhain's iron-alum-haematoxylin were used for staining, the former being more satisfactory.

THE DEVELOPMENT OF THE FLOWER

As in most inflorescences, the flower of *Martynia louisiana* arises as a lateral branch (FIG. 1, X) in the axil of a bract (FIG. 1, B). The first bract arises as a lateral papilla near the apex of the main axis of the raceme (FIG. 2, B′). This bract grows rapidly and about the time its tip reaches the apex of the raceme, a rather broad protuberance appears in the axil (FIG. 1, X). With further growth of the axis of the raceme other bracts appear, and in the axils of these the primordia of other flowers develop (FIG. 4, X). As the rudiment of

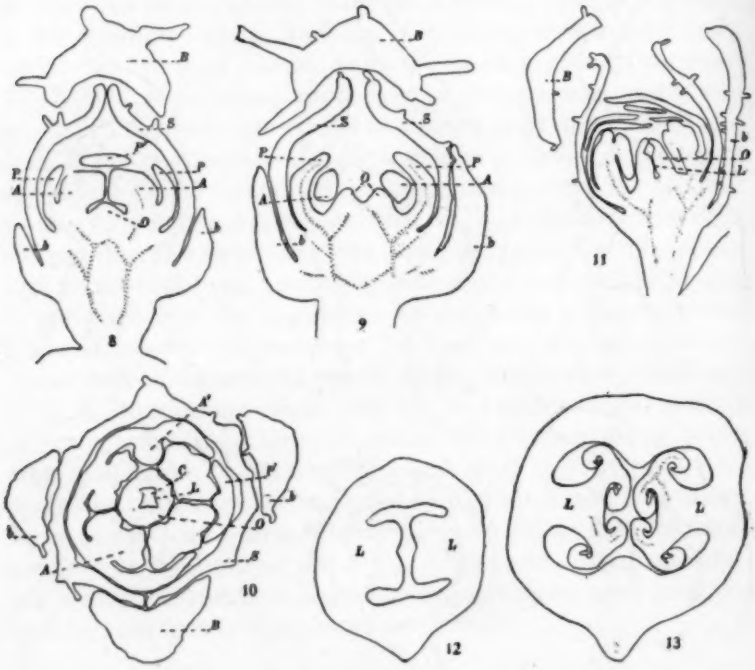
the flower grows it becomes broader and somewhat oblique at the apex (FIGS. 2 and 3, X). On the adaxial side of the primordium of the flower there appears a protuberance or ridge, the upper lobe of the calyx, extending about one third the distance around it (FIG. 3, S). Very soon the other lobes of the calyx appear as small protuberances similar to the adaxial lobe. The individual lobes appear as separate protuberances, but later grow up as a tube except on the abaxial side of



FIGS. 1–7. Development of the flower. FIGS. 1–3, × 45; FIGS. 3–7, × 30. B, bract; X, flower primordium; S, S', calyx lobe; P, corolla lobe; A, stamen; O, pistil; b, bracteole.

the flower. At this point, the two lower lobes of the calyx are united only at the base and in the mature flower overlap. The adaxial lobe of the calyx is the largest, and in the bud covers the other lobes (FIGS. 4 and 7, S). The calyx lobe, shown at S' in FIG. 4, is the edge of one of the lateral lobes and appears smaller than it really is. Just within the calyx lobes are seen small

protuberances (FIG. 4, P), the primordia of the corolla lobes, which are alternate with those of the calyx. Arising simultaneously with the corolla lobes (FIG. 5, P) and alternate with them are the epipetalous stamens (FIG. 5, A). FIGS. 6 and 7 are other sections of the flower shown in FIG. 5. FIG. 6 is a median section through the primordia of two lobes (P) of the corolla, while FIG. 7 is a median section through the primordia of two stamens (A). A comparsion of these two figures will give the relative size of the parts at this stage. There are primordia



FIGS. 8–13. Development of the flower (*con.*), × 30. B, bract; b, bracteole; S, calyx lobe; P, P^1, corolla lobe; A, A^1, stamen; O, pistil; L, placenta; C, ovarian cavity.

of five stamens, but very early the one between the posterior pair becomes aborted (FIGS. 10 and 14, A′). The pistil is the last cycle to appear, and in FIG. 5 is seen as a broad protuberance (O).

In FIGS. 5–9, at B, are seen cross sections of the bract which curves over the flower. These figures are of the flower as viewed from the adaxial side. And in the same figures at b, are seen sections of the two bracteoles. The two bracteoles arise as

protuberances similar to those of the lobes of the calyx, but earlier than the calyx lobes. The bracteoles develop inferior to the calyx, opposite each other and at right angles to the bract (FIG. 10, b, B). Since FIG. 9 is a median section through the flower, only the edge of each bracteole is shown. At this stage, they are large enough to cover the young flower.

FIGS. 8 and 9 show the further development of the parts of the flower. The calyx (S) is large enough to cover the other floral parts. An almost median section of two lateral lobes (P) of the corolla is shown in FIG. 9, while a cross section of the tip of the lower lobe is shown at P^1 in FIG. 8. The lower lobe of of the corolla is the largest and in the bud is covered by the others. The manner in which the corolla lobes overlap is shown in FIG. 11. A median section through two of the stamens (FIG. 8, A) of the same flower shows the further development of the stamens seen at A, FIG. 7. As in most cases, the development of the anther precedes that of the filament (FIG. 8, A). However, at this time the tissue of the anther is undifferentiated. At the time the pollen mother-cells are formed the filament is still shorter than the anther. The filaments remain short (FIG. 14) until almost the time of anthesis, when they elongate rapidly, bringing the anthers into the throat of the corolla, just below the lips of the stigma (FIG 16). The stamens are didynamous, the posterior pair being the longer. Just before anthesis, the lobes of the anther diverge, forming a straight line transverse to the filament. At the same time, the filaments of the corresponding pairs of stamens converge in such a way as to bring the diverging anthers into contact (FIG. 16) along the line of their linear dehiscence. At time of shedding, the rather large pollen grains are characterized by an exine that is thickened in the form of hexagonal areas.

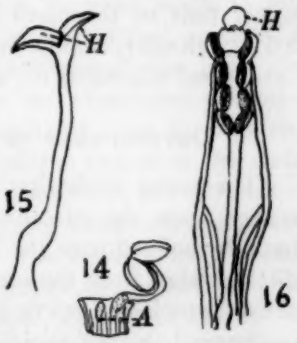


FIG. 14. Immature stamen. A, aborted stamen.

FIG. 15. Mature pistil, slightly enlarged. H, stigma lobes.

FIG. 16. Mature pistil and stamens in position. H, stigma lobes.

As was stated previously, the pistil appears as a rather broad protuberance (FIG. 5, O), but soon a depression is formed in the center (FIG. 9, O). The primordium of the pistil continues

to grow up as a ring enclosing a central ovarian cavity as is seen in cross section (FIG. 10, C). At a very early stage in the growth of the pistil, two parietal placentae appear. These are seen as outgrowths from the walls of the cavity (FIGS. 10 and 11, L). These outgrowths extend toward the center of the cavity and soon each forms two lobes (FIG. 12, L) which develop into the two lamellae of each placenta, resembling in cross section the letter T (FIG. 13, L). The placentae grow together at the base, thus forming a short columella. A cross section through the base of the ovary would appear as two-celled, but no ovules are developed from this region of the placentae. The upper part of the pistil is tubular and more narrow, forming a long, slender, hollow style which terminates in an unequally two-lipped stigma (FIG. 15, H).

DEVELOPMENT OF MEGASPORE AND EMBRYO-SAC

The young ovule first appears as a small, nipple-like protuberance upon the placenta. Very early in its development, a hypodermal cell near the tip becomes differentiated and may be distinguished from the surrounding cells by its large nucleus and dense cytoplasm (PLATE 7, FIG. 17). This cell, the megaspore mother-cell, grows rapidly, keeping pace with the lengthening nucellus. At this stage, the nucellus consists of merely the enlarged megaspore mother-cell, covered by the epidermis (FIG. 18). At the base of the nucellus the single integument appears as a fold, at first more pronounced on the side next to the cavity of the ovary (FIG. 18, I). By the more rapid growth of this side the ovule soon becomes sharply curved, so that the long axis of the nucellus is now parallel with that of the funiculus. At this stage, the integument extends around the nucellus, which has become more elongated (FIG. 19). With further growth the integument soon equals and finally exceeds the nucellus (FIGS. 20 and 21). The megaspore mother-cell has also grown rapidly and when fully developed is still enclosed by only a single layer of nucellus (FIG. 21). The nucleus, which has increased in size preparatory to the first division and which has had a position near the center of the cell (FIG. 20), comes to lie nearer the chalazal end, where it undergoes the first or heterotypic division (FIG. 21). All the spindles of this stage found were rather small as compared with the size of the cell. Whether cell formation follows this first nuclear division was not ascertained, but the

typical axial row of four megaspores is finally formed (FIG. 22), and, as is usually the case, the innermost megaspore, the one next the chalazal end, persists to form the embryo-sac (FIGS. 22 and 23). The upper three potential megaspores are soon destroyed by the rapid growth of the functional one (FIG. 23.)

By the time the tetrad is formed, the nucellus has reached its maximum growth, and the cells of the integument adjacent to the nucellus have become dense in cytoplasm and now function as a nutritive jacket (FIG. 22). In the meantime the integument has grown and exceeds considerably the length of the nucellus (FIG. 23).

The functional megaspore does not increase much in size before the first nuclear division but, after this first division, it elongates rapidly and occupies a space almost the length of the nucellus (FIGS. 23 and 24). As the megaspore elongates the two nuclei keep their relative positions—one in each end of the cell. Most of the cytoplasm of the cell is in the ends, thus leaving a large vacuole in the center. A few strands of cytoplasm penetrate the vacuole and form a connection between the masses at each end of the cell. The rapid growth of this cell has consumed the three upper potential megaspores and the nucellus around the center of the spore (FIG. 24). Before the second nuclear division of the megaspore takes place, the upper three megaspores have practically disappeared and the functional one now extends nearly the length of the nucellus, which is rapidly being used as food (FIG. 25). At this time the central vacuole is not so pronounced—at least in some cases. The spindles of the second nuclear division may be seen—one in each end of the cell. With the exception of a few cells at the chalazal end, the nucellus is consumed by the growing megaspore, which comes to occupy the space left by the disorganizing tissue. There is no evidence of a nucellar cap being formed as Merrell reported for *Silphium* (3) and other plants that have a similar development. The nuclei now undergo another division which results in eight nuclei—four in each end of the cell. Next follows the formation of the three cells of the egg-apparatus and the three antipodals. One nucleus from each end of the embryo-sac, the polar nuclei, remains free in the cytoplasm. At this stage, the embryo-sac is considerably elongated, being about seven times as long as wide. The micropylar end, containing the egg-apparatus, is enlarged to about one and a half times the diameter of the other part of the sac. This enlarged portion comprises nearly one

third the length of the embryo-sac. The egg-apparatus consists of the large pear-shaped egg-cell, which extends far down into the sac cavity, and the two large synergids (PLATE 8, FIG. 26, G and Sn). The lower part of the egg in which the nucleus lies is well filled with cytoplasm, but the upper part is vacuolate. The synergids, one on either side of the egg, extend down about two thirds the length of the egg-cell. Each synergid has a diameter nearly equaling that of the egg and a centrally located nucleus, which is a little smaller than the egg nucleus. As is frequently found in other angiosperms, a fairly large vacuole lies below the nucleus in the synergid (FIG. 26, Sn).

In the chalazal end of the embryo-sac are the three, rather long, slender, well-developed antipodals (FIG. 26, N). In most instances, the nuclei of the antipodals are fairly large and the cytoplasm has the character of that of the body of the embryo-sac.

After the formation of the cells at either end of the embryo-sac the polar nuclei move to the center and lie side by side for some time (FIG. 26, Pn), but before the pollen tube reaches the embryo-sac, the two polar nuclei fuse (FIG. 27). Sections were made of ovaries from flowers in which pollination had not occurred and it was found that the polar nuclei had fused (FIG. 28). So the fusion of the polar nuclei is in no way due to a stimulus from the pollen tube. The fusion nucleus does not approach the egg-apparataus, as Kanda reported for *Verbena* (**2**), but remains in the center of the embryo-sac. Each polar nucleus has a very prominent nucleolus and after fusion the two nucleoli are very noticeable for some time (FIG. 27), but later only one large nucleolus is usually seen (FIG. 28).

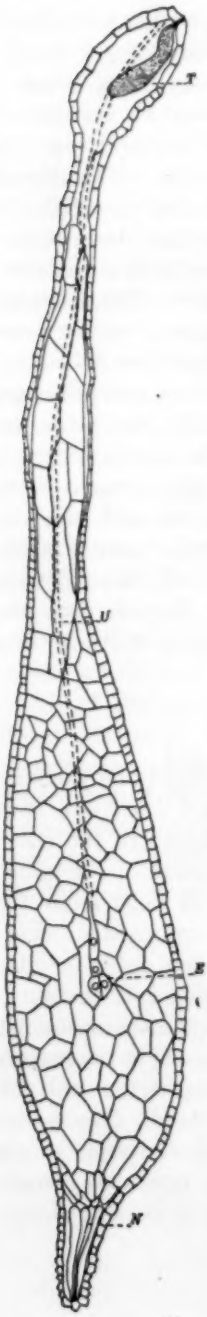
POLLINATION

The polar nuclei seem to unite about the time of anthesis, for conditions like those represented in FIG. 26 are observed in ovaries fixed just before the expansion of the corolla lobes, while the fusion nucleus is seen in flowers that have been open one or two hours. Most of the flowers open early in the morning, and shortly after daylight the bees, which are the chief pollinizing agents, are busy gathering nectar from the lower portion of the corolla tube.

The two lobes of the sensitive stigma stand open just above the open anthers (FIG. 16), in the upper portion of the throat of the corolla, and the bee, entering the corolla tube, brushes the stigma, thus depositing the pollen that may be present on the upper part of its body and securing a new supply from the open anthers just below as it walks down the tube. The stigma is very sensitive when the flower first expands and the slightest touch will cause the lobes to close. If pollen be present they usually remain closed, but, in the absence of pollen, they reopen in from five to ten minutes. If pollen is witheld the stigma lobes may be made to close and open many times, but after one to three days the stigmas tend to lose their sensitiveness. However, this sensitiveness is not an index to the receptiveness of the stigmatic surface, for flowers hand pollinated after the stigma ceased to be sensitive and even after the corolla dropped, produced viable seeds. Viable seeds were also secured from flowers hand pollinated in the bud before the stigma lobes normally opened. This was accomplished by gently forcing pollen between the closed lobes by means of a needle. In most flowers thus treated the stigma lobes never opened. At this time the anthers are still closed, but pollen from these as well as from open anthers was shown to be effective.

FERTILIZATION

Usually the pollen grains germinate immediately on the stigmatic surface, as was readily seen in material fixed one hour after the pollen was applied. At this time, many of the tubes were well into the tissue of the style. The growth of the pollen tube through the tissue, usually two or three cells from the stylar canal, is very rapid, for fertilization frequently occurs within six hours after pollination. The pollen tube is filled with plastids and granules that take such a dense stain that it is impossible to demonstrate the presence of the sperm nuclei, but, since the long, slender crescentic generative cell in the mature pollen grain shows only one nucleus, it is thought that the formation of the two sperms takes place in the tube. The pollen tube, as it grows nearly straight down through the style to the placenta, is comparatively broad and seems to retain its densely staining quality throughout the greater part of its length.



On reaching the ovule, the pollen tube grows through the micropyle and enters the embryo-sac, sometimes a little to one side, crushing one or both the synergids. The tip of the pollen tube usually covers the egg-cell, thus obscuring the nucleus of the latter (FIG. 32). In some instances it seems that the tube enters the egg-cell at the upper end and transverses the entire length of it (FIG. 31). In all cases observed, there was evidence that the tube had discharged the sperm nuclei in such a way that one of them came in direct contact with the egg nucleus (FIG. 30). Only the sperms and a little of the contents from the tip leave the pollen tube (FIGS. 30 and 31). The fate of the second sperm nucleus was not ascertained, but it seems evident that it plays no part in the formation of the endosperm. The second sperm nucleus may not leave the tube, but this point can not be demonstrated until some method of fixing and staining can be found that will reveal the presence of the nuclei among the granules in the cytoplasm. The pollen tube in the micropyle and in the upper part of the embryo-sac retains its form and densely staining quality long after the embryo-sac is filled with endosperm (FIG. 35).

The actual union of sperm and egg nucleus is similar to that in other angiosperms. The instances of fertilization observed were similar to that of *Lilium Martagon*, figured by Mottier (**4**). For *Verbena*, Kanda (**2**) figures the sperm nucleus in contact with the egg-cell and speaks of it as fertilization. In all the fertilization stages observed in *Martynia*,

FIG. 35. Embryo-sac filled with endosperm, × 140. T, pollen tube; N, antipodali; E, embryo; U, suspensor.

the sperm has been in direct contact withthe egg nucleus. This would seem to indicate that the pollen tube carries the sperm into the egg-cell.

THE ENDOSPERM

The primary endosperm nucleus, resulting from the union of the two polar nuclei, occupies a position near the center of the embryo-sac. Usually before the pollen tube enters the sac this endosperm nucleus divides and a transverse wall is formed between the two resulting nuclei, thus dividing the embry-sac into two chambers (FIG. 29). At this time, the cytoplasm in the embryo-sac has a frothy appearance due to the many small vacuoles present. This frothy character seems to appear after the fusion of the polar nuclei (FIG. 28). Very conspicuous, densely staining plastid primordia and granules are present in the cytoplasm. The synergids seem to have increased in length and to have become more vacuolate (FIG. 29). The egg-cell remains apparently unchanged. The antipodals are more elongated and sometimes contain a granular, densely staining cytoplasm (FIG. 29). After the wall dividing the embryo-sac into two chambers is formed, the nuclei move to a nearly central position in their respective cells. And, as one would infer, the endosperm cell at the micropylar end of the sac grows more rapidly than the one at the chalazal end (FIG. 31). The pollen tube usually reaches the embryo-sac when the endosperm is in a two-celled stage. In FIG. 31, it may be seen that fertilization has taken place. The outline of the tip of the pollen tube is shown by a dotted line in the lower part of the egg-cell, and the shading represents the relative density of the contents in different parts of the tube. Only the tip seems to have discharged its contents. A remnant of one synergid still shows. The synergids, if not crushed out by the entrance of the pollen tube, are soon absorbed. The endosperm cell in the micropylar end of the sac is very large and contains a large nucleus with irregular outline and a prominent nucleolus. Many plastids are still seen in the frothy cytoplasm of both endosperm cells, and some are present in the antipodals, which continue to grow, especially in length (FIG. 31). The increase in size of the antipodals is better illustrated in FIG. 32. Their cytoplasm is somewhat vacuolate at this stage and the large nuclei contain very prominent nucleoli. Usually the first division of the endosperm cell is transverse

and the second longitudinal, the one in the micropylar end dividing before the one in the chalazal end; but, in FIG. 32, it appears as if the first division had been longitudinal and the second transverse. The cytoplasm in the large cells around the fertilized egg contains many large as well as small vacuoles, while that of the lower cells contains only small ones. Very few plastids are present at this stage. They are seldom noticeable in later stages of endosperm development. FIG. 32 shows also the old densely staining pollen tube in the micropyle and upper end, of the embryo-sac, its tip covering the fertilized egg. By focusing down on the tip of the tube, the nucleus of the fertilized egg is seen and is represented in the drawing by a dotted line (FIG. 32). In the meantime, the whole embryo-sac has been enlarging at the expense of the integument which also has grown. The enlargement is more pronounced at first in the micropylar end where the fertilized egg is elongating. The layer of cells of the integument adjacent to the embryo-sac is always dense and rich in cytoplasm and functions as a nutritive jacket to the growing endosperm. FIG. 33 shows the further development of the endosperm, and the elongation of the fertilized egg. The old pollen tube is still very prominent in the micropyle and upper end of the sac, obscuring the upper portion of the fertilized egg-cell. The cytoplasm in the large endosperm cells of the micropylar end is very vacuolate, due probably to the rapid growth of the cells and to the loss of food to the developing embryo. Only a few endosperm cells develop in this end of the sac, for very soon a long suspensor is formed which brings the embryo into the chalazal end. The endosperm cells in the middle of the sac are smaller and richer in cytoplasm than the upper ones. The antipodals have nearly reached their maximum growth. They seem to function as elaborators of food and persist long after the embryo-sac is well filled with endosperm (FIG. 35). In several cases, four antipodals, all well developed, were found (FIG. 33). The extra one had probably been formed by the

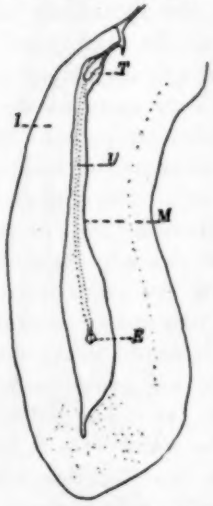


FIG. 36. Outline of ovule, × 44. I, integument; M, embryo-sac E, embryo; U, suspensor; T, old pollen tube.

division of one of the three normal ones. FIG. 34, a cross section of the chalazal end of an embryo-sac in the same stage as the above, shows the arrangement of the four antipodals. At this stage, the nuclei of the antipodals appear as densely staining homogeneous masses.

As the embryo with its very long suspensor grows through the center of the elongating embryo-sac, large endosperm cells rich in cytoplasm are formed, but when it reaches the lower part of the sac where the first division of the embryo takes place, the endosperm growth practically ceases in the middle and upper part of the sac. The cells of this part of the sac are rather large and similar in shape to those first formed, while those in the lower part are smaller and not so rich in cytoplasm (FIG. 35). It is also seen from FIG. 35 that the embryo-sac has enlarged considerably, especially the lower part which contains the developing embryo. The nutritive jacket is still very active in the elaboration of food for the growing endosperm. FIG. 36 shows in outline the relative size of the embryo, endosperm and integument at the time the embryo is in the two-cell stage as seen in FIG. 35.

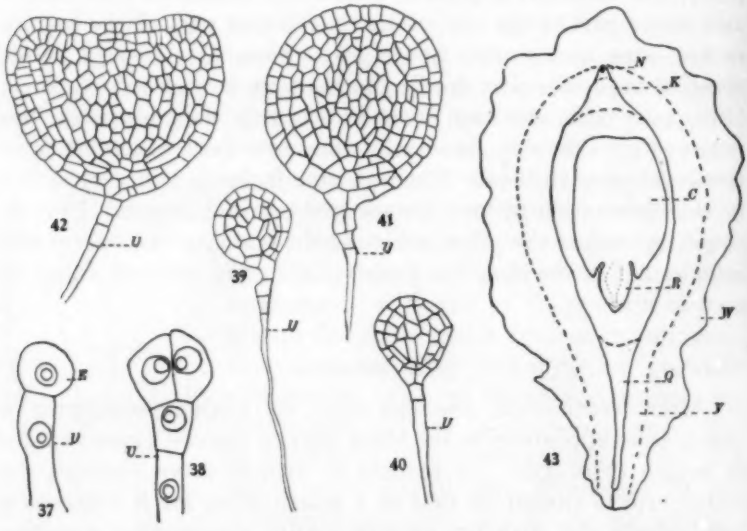
THE EMBRYO

After fertilization, the egg with its nucleus occupying a nearly central position in the lower part of the cell grows rapidly in length (FIG. 33). Its manner of growth down through the endosperm is similar to that of a pollen tube, for it becomes a long narrow cell with the nucleus retaining a position near the growing tip. No division seems to take place until the distal end has transversed nearly two thirds the length of the embryo-sac. The lower portion of the cell is rather dense in cytoplasm and stains deeply, but the upper portion has very little and stains so faintly that the course of its growth is hard to trace.

After the distal end has reached the lower portion of the embryo-sac, a transverse division occurs, which forms a very long, slender suspensor cell and a short, rounded distal one, the embryonal cell (FIG. 37). In most instances the cytoplasm of the embyonal cell contains many plastids and other densely staining granules, while that of the suspensor is very poor in plastids. After the first division two others occur almost simultaneously. The suspensor cell divides, forming a short cell next the embryonal cell, which has enlarged preparatory to division, and, at the

same time, the enlarged embryonal cell divides longitudinally forming a two-celled embryo (FIGS. 38 and 35). The second division of the embryo is usually transverse and the third longitudinal, thus forming the octant stage The further growth of the embryo is illustrated in FIGS. 39–43 and is so like the well known development of *Capsella* that details are unnecessary.

The very long suspensor, shown in Fig. 35 in dotted lines, is almost indentical with that of *Trapella sinensis* Oliv. as figured by Oliver (**5**, *pl. 7, f. 36*). The suspensor of *Myoporum*



FIGS. 37–43. Development of the embryo. FIGS. 37–38, × 500; FIGS. 39–42, × 175; FIG. 43, × 6. E, embryo; U, suspensor; C, cotyledon; R, radicle; K, chalazal end of embryo-sac; Q, micropylar end of embryo-sac; N, remains of antipodals; V, soft, inner portion of seed coat; W, hard, warty portion of seed coat.

serratum as figured by Billings (**1**, *f. 51*) is also similar in structure but does not push the embryo as far down into the embryo-sac as that of *Martynia*, although the shape of the embryo-sac and the development of the endosperm are much the same in both species. Usually a second and sometimes a third division occurs in the suspensor, resulting in two or three short cells next the embryo, the innermost of which seems to contribute to its formation.

FIG. 43 shows a section of a young seed containing a nearly mature embryo. The radicle (R) is short and thick while the

cotyledons (C) are very large and fleshy. This figure shows also a little endosperm which, in the mature seed, comprises a thin, transparent covering for the embryo. The embryo has developed in such a way that it practically fills the lower part of the sac, while the upper and middle portions (Q) form in the mature seed a little brown tube on the micropylar end of the remaining endosperm. There is also a small brown knob at the chalazal end (K) marking that part of the embryo-sac formerly occupied by the large antipodals, the remains of which appear at N. The broken line in this figure represents the demarcation in the tissue forming the seed coat. That region of tissue next the endosperm (V) matures into the soft inner portion of the seed coat, while the walls of the cells forming the outer portion (W) become thick and lignified, thus maturing into a hard warty exterior which becomes very dark brown or black in color.

SUMMARY

The flowers develop in the axils of protective bracts. The cycles of the flower appear in the following order: calyx, corolla and epipetalous stamens, and pistil.

Of the four potential megaspores formed, only one is functional.

The embryo-sac is long and narrow, with the micropylar end considerably enlarged. The large egg-cell extends far down into the sac cavity, with the two synergids on either side. The three antipodals are long, slender cells that increase in size and persist as elaborators of food.

The polar nuclei move to a position near the center of the sac where they unite before the pollen tube reaches the ovule.

Fertilization usually occurs within six to eight hours after pollination.

The rather large pollen tube stains densely throughout the greater part of its length and persists in the micropyle and upper end of the embryo-sac long after the endosperm is formed.

The first division of the endosperm cell, which is usually transverse, occurs before fertilization. At first, a few cells are formed in the upper and middle portions of the embryo-sac, but the bulk of the endosperm is in the lower part of the sac, where the embryo develops.

The suspensor is very long and narrow and pushes the embryo

into the lower portion of the embryo-sac, where the first division takes place. The development of the embryo proper is like that of *Capsella*.

I take opportunity here to express my obligations to Professor H. W. Anderson for the use of the Wabash College Botanical Laboratory during the summers of 1915 and 1916 and to Professor D. M. Mottier for valuable assistance and criticism in connection with this study.

INDIANA UNIVERSITY

LITERATURE CITED

1. **Billings, Frederick H.** Beiträge zur Kenntniss der Samenentwickelung. Flora **88**: 253–318. 1902.

2. **Kanda, M.** Field and laboratory studies of *Verbena*. Bot. Gaz. **69**: 54–71. *pl. 6–9 + f. 10–17, 27, 54–63, 69–75*. 1920.

3. **Merrell, W. D.** A contribution to the life history of *Silphium*. Bot. Gaz. **29**: 99–133. *pl. 3–10*. 1900.

4. **Mottier, D. M.** Fecundation in plants. Carnegie Inst. Washington Publ. 15. 1904.

5. **Oliver, F. W.** On the structure, development, and affinities of *Trapella*, Oliv., a new genus of Pedalineae. Ann. Bot. **2**: 75–115. *pl. 5–9*. 1888.

Explanation of plates 7 and 8

PLATE 7

All figures, × 400

FIG. 17. Vertical section through the nucellus; megaspore mother-cell shaded.

FIG. 18. Elongated nucellus with megaspore mother-cell; beginning of integument, 1.

FIG. 19. Vertical section of young ovule turned on its axis; the integument reaching half the length of the nucellus.

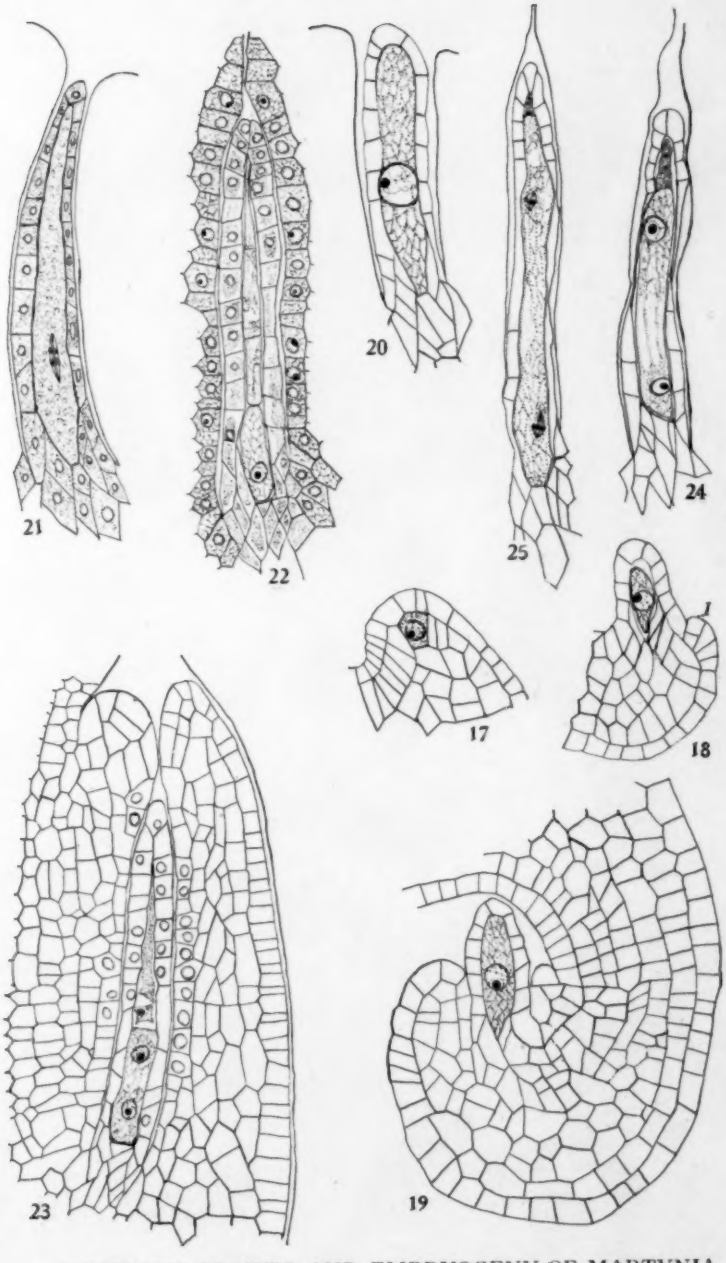
FIG. 20. Nearly mature megaspore mother-cell enclosed in a single layer of nucellus.

FIG. 21. Heterotypic spindle in megaspore mother-cell.

FIG. 22. Tetrad, the upper three potential megaspores disorganizing. Nutritive jacket formed from the layer of integument adjacent the nucellus.

FIG. 23. Section of young ovule showing the single integument and first division of the megaspore; the upper three potential megaspores disorganizing.

FIGS. 24 and 25. Further development of the megaspore; the central portion of nucellus disorganizing.



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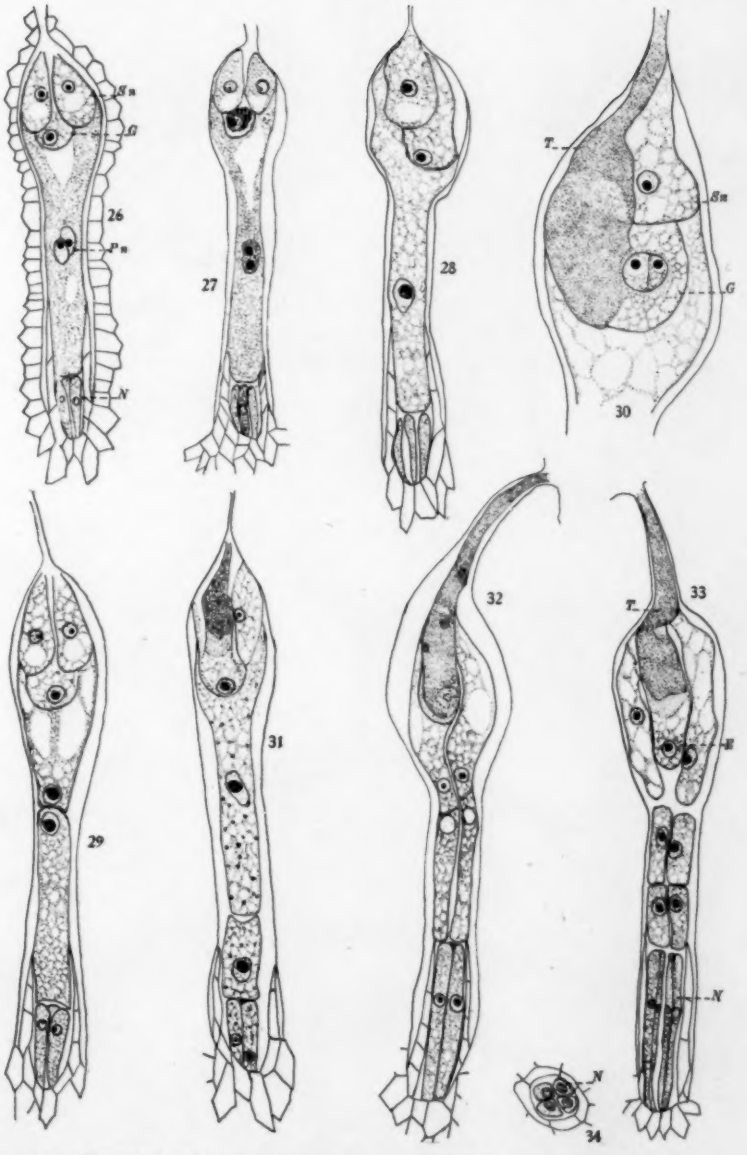

ANDERSON: FLOWER AND EMBRYOGENY OF MARTYNIA

PLATE 8

FIGS. 26–33, longitudinal sections of embryo-sacs. FIG. 34, cross section of antipodals.

FIG. 26. Mature embryo-sac; polar nuclei side by side near the center of the sac; G, egg-cell; Sn, synergid; N, antipodals; Pn, polar nuclei, × 300.

FIG. 27. Mature embryo-sac; polar nuclei fusing, × 300.

FIG. 28. Mature embryo-sac; polar nuclei fused, × 350.

FIG. 29. Endosperm two-celled; egg not yet fertilized, × 350.

FIG. 30. Fertilization. Sperm and egg nuclei in contact; old pollen tube quite prominent; G, egg-cell; T, pollen tube; Sn, synergid, X 740.

FIGS. 31 and 32. Development of endosperm and elongation of antipodals, X 350.

FIG. 33. Development of endosperm and embryo; four antipodals, N; E, elongating embryo; T, old pollen tube, × 350.

FIG. 34. Cross section of chalazal end of embryo-sac showing four antipodals, N, × 350.

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1921

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Adams, J. F. Observations on the spores of *Sichzophyllum commune*. Torreya **21**: 98–100. D 1921. [Illust.]

Allen, W. E. Some work on marine phytoplankton. Trans. Am. Micr. Soc. **40**: 177–181. O 1921.

Allen, W. E. The investigation of ocean pasturage. Ecology **2**: 215–219. 3 D 1921.

Ames, O. Additions to the orchid flora of Panama. Proc. Biol. Soc. Washington **34**: 149–154. 21 D 1921.

Includes 7 new species.

Ames, O. *Eria gigantea*. Gigantic eria. Addisonia **6**: 41, 42, *pl. 213*. 24 O 1921.

Anderson, E. G. The inheritance of salmon silk color in maize. Cornell Univ. Agr. Exp. Sta. Mem. **48**: 539–554. N 1921.

Anderson, P. J., & Ickis, M. G. Massachusetts species of *Helvella*. Mycologia **13**: 201–229. *pl. 11, 12*. 8 O 1921.

Arthur, J. C. Memoranda and index of cultures of Uredineae, 1899–1917. Mycologia **13**: 230–262. 8 O 1921.

Ashe, W. W. Notes on *Rhododendron*. Rhodora **23**: 177–179. 24 O 1921.

Bailey, L. H. *Magnolia stellata.* Addisonia **6**: 37, 38. *pl. 211.* 24 O 1921.

Ball, C. R. Notes on willows of sections *Pentandreae* and *Nigrae.* Bot. Gaz. **72**: 220–236. *f. 1–4.* 15 O 1921.

Includes 2 new varieties of *Salix* from California.

Barker, E. E. Bud variation in the sugar cane. Jour. Hered. **12**: 271–274. *f. 27.* 23 S 1921.

Bechtel, A. R. The floral anatomy of the Urticales. Am. Jour. Bot. **8**: 386–410. *pl. 15–22.* 14 N 1921.

Bird, H. Soil acidity in relation to insects and plants. Ecology **2**: 193–197. 3 D 1921.

Birge, E. A., & Juday, C. Further limnological observations on the Finger Lakes of New York. Bull. Bur. Fisheries **37**: 211–252. *f. 1–5.* 8 O 1921.

Includes notes on plankton botany.

Blakeslee, A. F., Cartledge, J. L., & Welch, D. S. Sexual dimorphism in *Cunninghamella.* Bot. Gaz. **72**: 185–219. *f. 1.* 15 O 1921.

Boynton, K. R. *Bergenia crassifolia.* Thick-leaved saxifrage. Addisonia **6**: 43. *pl. 214.* 24 O 1921.

Boynton, K. R. *Helichrysum bracteatum.* Strawflower. Addisonia **6**: 46. *pl. 215.* 24 O 1921.

Bradshaw, R. V. *Cynosurus echinatus* in Oregon. Torreya **21**: 81–83. O 1921.

Braun, E. L. Composition and source of the flora of the Cincinnati (Ohio) region. Ecology **2**: 161–180. *f. 1.* 3 D 1921.

Briggs, G. Para and *Paspalum*: two introduced grasses of Guam. Guam Agr. Exp. Sta. Bull. 1: 1–44. *pl. 1–6.* 2 D 1921.

Britton, E. G. *Clerodendron Thompsonae.* Mrs. Thompson's clerodendron. Addisonia **6**: 39, 40. *pl. 212.* 24 O 1921.

Britton, N. L. *Lathyrus latifolius.* Everlasting pea. Addisonia **6**: 35. *pl. 210.* 24 O 1921.

Britton, N. L. Plant nomenclature: more suggestions. Jour. Bot. **59**: 296, 297. O 1921.

Brotherston, R. P. The pentstemon. Gard. Chron. **70**: 208. 22 O. 1921.

Burlingame, L. L. Variation and heredity in *Lupinus*. Am. Nat. **55**: 427–448. *f. 1–3.* O 1921.

Cayla, V. A propos de la qualité du cauotchouc d'*Hevea brasiliensis*, ses variations, leurs causes. Importance economique pour la production de l'Amazone. Arch. Escol. Super. Agr. e Med. Veter. **5**: 81–96. S 1921.

Chace, E. M., Wilson, C. P., & Church, C. G. The composition of California lemons. U. S. Dept. Agr. Bull. 993: 1–18. *f. 1–4.* 15 O 1921.

Chamberlain, C. J. Growth rings in a monocotyl. Bot. Gaz. **72**: 293–304. *f. 1–16.* 15 N 1921.

Clark, A. H. A new classification of animals. Bull. Instit. Oceanogr. 400: 1–24. 20 S 1921.

Includes a summary of plant classification.

Clements, F. E. Drouth periods and climatic cycles. Ecology **2**: 181–188. 3 D 1921.

Coker, W. C., & Beardslee, H. C. The collybias of North Carolina. Jour. Mitchell Sci. Soc. **37**: 83–107. *pl. 1 + f. 4–23.* D 1921.

Includes *Collybia lilacina*, sp. nov.

Cook, F. C. Absorption of copper from the soil by potato plants. Jour. Agr. Research **22**: 281–287. 29 O 1921.

Cook, M. T. The blossom blight of the peach. Phytopathology **11**: 290–294. *pl. 12.* 15 N 1921.

Cook, M. T. Falling foliage. Phytopathology **11**: 337–339. 9 D 1921.

Cook. M. T. Peach yellows and little peach. Bot. Gaz. **72**: 250–255. *pl. 6, 7.* 15 O 1921.

Cook, M. T. Wilting caused by walnut trees. Phytopathology **11**: 346. 9 D 1921.

Cook, O. F. Causes of shedding in cotton. Jour. Hered. **12**: 199–204. *f. 3–6.* 23 S 1921.

Coville, F. V. Directions for blueberry culture, 1921. U. S. Dept. Agr. Bull. 974: 1–24. *pl. 1–29.* 15 O 1921.

Creswell, C. F., & Bidwell, G. L. Composition of cotton seeds. U. S. Dept. Agr. Bull. 948: 1–221. *pl. 1 + maps 1–11.* 10 S 1921.

Dana, B. F. Two new *Sclerotinia* diseases. Phytopathology **11**: 225–228. *pl. 8.* 6 O 1921.

Doolittle, S. P. Overwintering of the bacterial wilt of cucurbits. Phytopathology **11**: 299, 300. 15 N 1921.

Dupler, A. W. The air chambers of *Reboulia hemisphaerica*. Bull. Torrey Club **48**: 241–252. *f. 1–22.* 13 D 1921.

Ehlers, J. H. *Panicum virgatum* var. *cubense* in Michigan. Rhodora **23**: 200. 15 D 1921.

Eldridge, A. E. Woodland flowers of the prairie region. Am. For. **27**: 714–716. N 1921. [Illust.]

Emerson, F. W. Subterranean organs of bog plants. Bot. Gaz. **72**: 359–374. *f. 1–11.* 15 D 1921.

Emerson, R. A. Genetic evidence of aberrant chromosome behavior in maize endosperum. Am. Jour. Bot. **8**: 411–424. *f. 1.* 14 N 1921.

Ensign, M. R. Area of vein-islets in leaves of certain plants as an age determinant. Am. Jour. Bot. **8**: 433–441. *pl. 23.* 19 D 1921.

Evans, A. W. The genus *Riccardia* in Chile. Trans. Connecticut Acad. Sci. **25**: 93–209. *f. 1–13.* D 1921.

Includes 3 new species and 17 new combinations.

Fairman, C. E. The fungi of our common nuts and pits. Proc. Rochester Acad. Sci. **6**: 73–115. *pl. 15–20.* S 1921.

Includes *Schizocapnodium*, gen. nov., and 27 new species in various genera.

Fehlinger, H. Brasilianische Faserpflanzen. Tropenpflanzer **24**: 173–176. D 1921.

Fujioka, M., & Takahaski, K. On the cause of the darkening of the heartwood of *Cryptomeria japonica* Don. Jour. For. **19**: 844–866. D 1921.

Gardner, G. A. Observations sur les articles du Reverend Père Fontanel, S. J. Nat. Canad. **48**: 49–56. S 1921.

Gardner, M. W., & Gilbert, W. W. Field tests with cucumber angular leafspot and anthracnose. Phytopathology **11**: 298, 299. 15 N 1921.

Gardner, M. W., & Kendrick, J. B. Soybean mosaic. Jour. Agr. Research **22**: 111–113. *pl. 18 19.* 8 O 1921.